A Phylogenetic Analysis of the Sirenia

Daryl P. Domning

Laboratory of Paleobiology, Department of Anatomy, Howard University, Washington, D.C. 20059

ABSTRACT.—Analysis of 62 cranial and dental characters of 36 species and subspecies of sirenians, by means of the Hennig86 computer program without character weighting, produced 60 maximally parsimonious trees (length 152, consistency index 0.55, retention index 0.83). With successive character weighting, these were reduced to six maximally parsimonious trees, of which the Nelson consensus tree is presented here (length 162, consistency index 0.76, retention index 0.91). Sample size and intrapopulational variation are insufficiently studied problems in cladistic analysis, and a statistically based method for scoring variable characters is introduced. The tree's topology is least certain in three groups of taxa: Eocene dugongids, dugongines (here including rytiodontines), and species of *Metaxytherium*. The most novel results of this study: (1) The Miosireninae are the sister group of the Trichechidae as previously defined, and are here placed in that family; a subfamily Trichechinae is formally erected for the remaining trichechids. (2) The Trichechidae in this broader sense appear to have arisen somewhat later than previously supposed (late Eocene or early Oligocene rather than middle Eocene) and are rooted well within the Dugongidae instead of being derived separately from the Protosirenidae. (3) *Dugong* lies within the clade heretofore called the Rytiodontinae, on the basis of the first strong evidence of where among the Dugongidae the living dugong's phyletic affinities lie. The name Dugonginae is extended to this entire clade in place of the junior name Rytiodontinae. Except within the Dugonginae, age rank and clade rank are highly correlated, suggesting that the fossil record provides a good picture of the history of the Sirenia. A revised provisional classification is proposed for the sirenian taxa analyzed here.

INTRODUCTION

The first formal cladogram of the order Sirenia to be published was that of Savage (1977). Since then, cladistic analyses have been presented for several subsets of the order: the Trichechidae (Domning and Hayek 1986), the Rytiodontinae (Domning 1989a,b, 1990), and the European species of *Metaxytherium* (Domning and Thomas 1987). In this paper I revise and extend this previous work to encompass all of the better-known Sirenia.

This study has been done in the context of much recent work that strongly supports the strict monophyly (= holophyly) of the order Sirenia and its membership in a supraordinal group (Tethytheria) with the Proboscidea and Desmostylia (e.g., Domning et al. 1986; Shoshani 1986; Tassy and Shoshani 1988; Novacek 1990; Thewissen and Domning 1992; and references cited therein). Although a few characters of the order gleaned from these studies are noted here, I do not review this body of work in detail or attempt to identify the sister group of the Sirenia but instead refer the reader to these sources for evidence on the relationships of sirenians to other mammals.

This paper is a preliminary report, based on a systematic revision still in progress.

MATERIALS AND METHODS

Thirty-six species and subspecies of sirenians were analyzed. Several other nominal species were excluded because they are known only from very incomplete material, because I have not examined the original specimens, and/or because I have serious doubts about their validity. For example, *Thalattosiren petersi* (Abel, 1904) was excluded because I suspect that the known skulls may represent merely immature *Metaxytherium*.

Moeritherium (Proboscidea) and *Paleoparadoxia* (Desmostylia) were used as outgroups for polarization of characters because of the evidence (cited above) that these two orders are the closest relatives of the Sirenia and because these genera are the most primitive adequately known members of their respective orders. However, both of these are apparently derived, relative to other mammals, in their imperforate lacrimals and single-rooted canines, whereas early sirenians display the primitive states (possession of a lacrimal foramen and double-rooted canines, respectively). More primitive proboscideans and desmostylians are known (anthracobunids and *Behemotops*, respectively; see Ray, Domning, and McKenna 1994, this volume) but are represented at present by

little or no cranial material and cannot be scored for most of the characters used here.

This analysis is based on some 108 morphological characters of the skull, mandible, and dentition (excluding cheek-tooth cusp patterns) that I have examined in detail in almost all of the known taxa of fossil and living sirenians. Of these 108 characters, I eliminated 46 that I was unable to score consistently or that were cladistically uninformative for the taxa included here (e.g., because they vary only in taxa that were excluded). The 62 informative characters (Table 1) were analyzed with the Hennig86 computer program (Farris 1988). Three multistate characters were treated as unordered because in these cases I had significant doubts that the states formed a single transformation series. Some other significant cranial and postcranial characters not used in the analysis corroborate and supplement certain parts of it.

Two aspects of cladistic data sets that are normally ignored are explicitly addressed here: sample size and intraspecific variation. Table 1 lists for each taxon the largest number of specimens examined for which any character could be scored. For any given character, the actual number of specimens scored was often much less than this maximum; however, separate citation of a sample size for each character of each taxon [as Domning and Thomas (1987) did for a much smaller data set] would have made the table prohibitively large and cumbersome. The present compromise at least provides an approximation of the sample sizes available for this study. As for variation, since Hennig86 does not accept multiple states of a character for a given taxon, polymorphisms had to be scored unambiguously as one of two states. The following procedure was adopted.

For the available samples, confidence limits for proportions and critical values of sample fractions (Xin = frequency of a state in a sample of size n) were determined (these are given in graphic or tabular form in standard statistics tables), using a confidence coefficient of 0.95. For example, if four specimens in a sample of five display a derived state, $Xin = 4/5 = 0.8$. The probability that the frequency of occurrence of the derived state in the *sampled population* was between 0.995 and 0.284 (the 95% confidence limits) is 0.95. (I here designate the lower confidence limit, 0.284 in this example, as the LCL_{95}.)

If a state (either primitive or derived) was present in the majority of the sample and its $LCL_{95} > 0.5$, the taxon was scored as having that state. If the majority state had an $LCL_{95} \le 0.5$, the scoring depended on the taxon's position relative to the character's distribution in the trees obtained from preliminary analyses: the

taxon was scored whichever way was more congruent with other characters (i.e., whichever way did not imply a reversal). If the sample was evenly divided, it was likewise scored as having the congruent state. If the taxon lay at the borderline of the character transformation (so that neither scoring choice would imply a reversal), it was scored as having the majority state. If it was both located at the borderline and evenly divided, it was scored as having the more primitive state (this is arbitrary; the opposite rule was tried also, but in this analysis the choice did not affect the geometry of the final tree). The rationale and implications of this procedure are discussed below (see under Comments on Methods).

CHARACTERS USED

The following 62 characters are those that have proven most informative and were used in the computer analysis, out of 108 characters (assigned numbers between 1 and 158) that I have studied in some detail. For simplicity of record-keeping, the numbers originally assigned to these characters are retained here. Numbers are not assigned to some other cranial characters whose only effect would be to define terminal taxa or strengthen nodes already adequately supported, as in the case of the hydrodamalines; these characters would therefore have no effect on the geometry of the final tree, though they would alter the tree's statistics. Likewise unnumbered are postcranial characters, because data on these are missing for many taxa. None of these unnumbered characters was included in the computer analysis, though they are listed below at the appropriate nodes. The data matrix for the 62 included characters is shown in Table 1. As usual, 0 designates the most primitive state observed among the taxa studied.

3. *Rostrum*: (0) small relative to cranium; (1) enlarged (length of premaxillary symphysis > 0.27 × condylobasal skull length) (see Fig. 1). (The ratio 0.27, like other ratios used below, was chosen because it separates what appear visually to be significantly different character states.)

6. *Nasal process of premaxilla*: (0) thin and tapering at posterior end, having lengthy overlap with frontal and/or nasal; (1) broadened and bulbous at posterior end, having more or less vertical joint surface in contact with frontal (Domning 1989a,b).

7. *Nasal process of premaxilla*: (0) long; (1) very short (see Fig. 1).

8. *External nares*: (0) not retracted; (1) retracted and enlarged, reaching to or beyond the level of the anterior margin of the orbit.

9. *Premaxilla*: (0) does not contact frontal; (1) contacts frontal.

11. *Zygomatic–orbital bridge of maxilla*: (0) nearly level with palate; (1) elevated above palate, with its ventral surface lying > 1 cm above the alveolar margin (cf. Domning 1978: fig. 8).

13. *Infraorbital foramen*: (0) small (about 15 × 10 mm or less); (1) large (greater than 15 × 10 mm).

14. *Zygomatic–orbital bridge of maxilla*: (0) long anteroposteriorly (vertical thickness < 0.40 × minimum length); (1) shortened (thickness 0.40 × length; cf. Domning 1978: fig. 24); (2) shortened and transformed into transverse vertical wall (Domning 1989b).

16. *Palate*: (0) thin or incomplete at level of penultimate cheek tooth; (1) > 1 cm thick at level of penultimate tooth.

31. *Nasals*: (0) meet in midline; (1) separated in midline by frontals or an incisure, or absent.

32. *Nasals*: (0) large (length of internasal suture 0.5 × length of interfrontal suture exposed dorsally); (1) smaller, or separated in midline, or absent.

36. *Supraorbital process of frontal*: (0) well developed, with prominent, dorsoventrally flattened posterolateral corner; (1) dorsoventrally thickened, with posterolateral corner variably developed; (2) reduced, rounded, lacking posterolateral corner (see
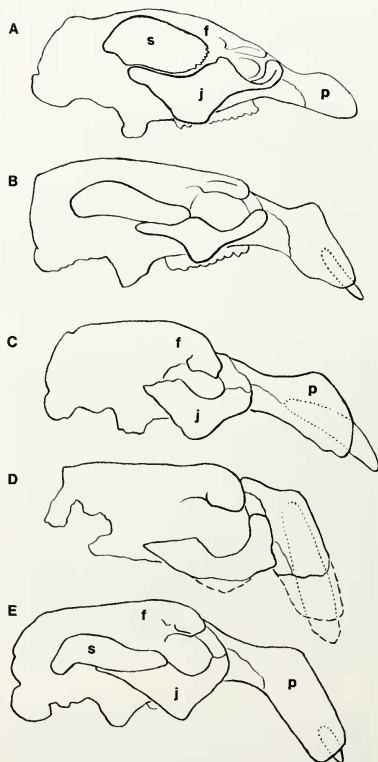

Figure 1. Skulls of sirenians in right lateral view, illustrating eight of the characters of the anterior part of the skull used in this analysis. Not drawn to same scale. See text for explanations of characters and states. Dashed lines indicate parts restored; dotted lines outline tusks within alveoli. Abbreviations: f, frontal; j, jugal; p, premaxilla; s, zygomatic process of squamosal. A, *Trichechus senegalensis*: 3(0), 7(0), 36(0), 43(0), 85(0), 89(0), 139(1), 140(0). B, *Halitherium schinzii*: 3(1), 7(0), 36(0), 43(0), 85(1), 89(0), 139(0), 140(1). C, *Dioplotherium manigaulti*: 3(1), 7(0), 36(— or 1), 43(1), 85(2), 89(1), 139(0), 140(2). D, *Rytiodus* sp.: 3(1), 7(1), 36(— or 1), 43(1), 85(2), 89(0), 139(0), 140(2). E, *Metaxytherium floridanum*: 3(1), 7(0), 36(1), 43(0), 85(2), 89(0), 139(0), 140(0).

Fig. 1; state 2 not illustrated). (This character was treated as inapplicable to "rytiodontines" because these follow a somewhat different transformation series, here expressed by character 43; however, it

would probably be equally correct, and would not alter the tree's topology, if all of these taxa were scored 1 for this character.)

37. *Nasal incisure* at posterior end of mesorostral fossa: (0) absent or small (does not extend posterior to the supraorbital process); (1) deep and narrow (extends posterior to the supraorbital process); (2) comparably deep but broad, with the anterior frontal margin displaying a median convexity. (Unordered character.)

38. *Lamina orbitalis of frontal*: (0) thin or absent; (1) 1 cm thick.

42. *Frontal roof*: (0) convex, or more or less flat between temporal crests (if latter present); (1) deeply concave, sloping steadily ventrad to anterior margin (cf. Domning 1990: fig. 4E).

43. *Supraorbital process of frontal*: (0) flattened in more or less horizontal plane, with dorsal surface inclined relatively gently ventrolaterad; (1) turned markedly downward, with dorsal surface inclined strongly ventrolaterad and posterolateral corner projecting posteriorly (see Fig. 1; Domning 1989a,b, 1990).

51. *Sagittal crest*: (0) present; (1) absent.

66. *Exoccipitals*: (0) meet in a suture dorsal to foramen magnum; (1) do not meet in a suture (this is a reversal to the condition found in primitive mammals; Shoshani 1986).

67. *Supracondylar fossa of exoccipital*: (0) absent; (1) distinct but shallow, directly dorsal to condyle; (2) deep and extending across entire width of occipital condyle; (3) reduced and located dorsomedial to condyle, or lost.

70. *Dorsolateral border of exoccipital*: (0) rounded and more or less smooth, not flangelike; (1) thick and overhanging posteriorly as a flange; (2) greatly thickened, forming rugose overhanging flange (Domning 1978; Domning and Hayek 1986).

73. *Posttympanic process of squamosal*: (0) absent (i.e., no facet projecting for sternomastoid muscle); (1) present; (2) enlarged and clublike.

74. *Sigmoid ridge of squamosal*: (0) present and prominent; (1) reduced or absent (cf. Domning 1978: fig. 7).

75. *External auditory meatus of squamosal*: (0) long mediolaterally (> 1 cm); (1) short (1 cm).

76. *Squamosal*: (0) does not extend to temporal crest; (1) extends to temporal crest.

77. *Processus retroversus of squamosal*: (0) absent; (1) present, moderately inflected; (2) present, not inflected (cf. Domning 1978: fig. 7). In *Dugong dugon*, it is strongly inflected (an autapomorphy). (Unordered character.)

82. *External auditory meatus of squamosal*: (0) narrow and slitlike (anteroposterior breadth less than dorsoventral); (1) about as wide anteroposteriorly as high; (2) very broad and shallow, wider anteroposteriorly than high.

84. *Zygomatic process of squamosal*: (0) medial side not swollen, appears relatively flat or concave and inclined inward dorsally; (1) medial side markedly swollen, inclined inward ventrally or forming a vertical wall (Domning and Hayek 1986).

85. *Ventral extremity of jugal*: (0) lies posterior to orbit; (1) lies approximately under posterior edge of orbit, but forward of jugal's postorbital process (if present); (2) lies ventral to orbit (see Fig. 1).

87. *Preorbital process of jugal*: (0) does not contact premaxilla; (1) contacts premaxilla.

88. *Preorbital process of jugal*: (0) relatively flat and thin (posteromedial-anterolateral breadth of portion lateral to maxillojugal suture > anteromedial-posterolateral thickness); (1) thick and robust (breadth thickness).

89. *Posterior (zygomatic) process of jugal*: (0) as long as or longer than diameter of orbit; (1) shorter than diameter of orbit (see Fig. 1).

91. *Lacrimal*: (0) with foramen (nasolacrimal canal); (1) without foramen, but still large; (2) vestigial or absent.

97. *Posterior border of palatine*: (0) not incised, merely shal-lowly concave; (1) incised or deeply indented; (2) very deeply incised, to as far forward as level of M^1.

99. *Palatines*: (0) extend anteriorly beyond posterior edge of zygomatic–orbital bridge; (1) do not extend so far forward.

101. *Alisphenoid canal*: (0) present; (1) absent. (Though this polarity is debatable in mammals generally, it is well supported for the Paenungulata, including the taxa considered here; Thewissen and Domning 1992.)

102. *Pterygoid fossa*: (0) absent; (1) present. (The polarity of this character is problematical, in view of the fossa's evident presence in *Prorastomus* but absence in *Paleoparadoxia* and *Protosiren*. This character is also scored 0 in *Moeritherium*, but this is apparently variable, as the fossa is present in one specimen but absent in another; J. Shoshani and J. G. M. Thewissen, pers. comm.)

103. *Foramen ovale*: (0) enclosed by bone; (1) opened to form a notch or incisure (this is a reversal to the condition found in primitive mammals; Novacek 1990).

115. *Periotic*: (0) fused to alisphenoid; (1) not fused with any other skull bone, set in closely fitting socket in squamosal.

121. *Mandibular symphysis*: (0) laterally compressed, with narrow masticating surface scarcely wider than the two rows of tooth alveoli it bears; (1) broad.

122. *Ventral border of horizontal mandibular ramus*: (0) straight or only slightly concave; (1) moderately concave, sharply downturned anteriorly; (2) moderately and evenly concave; (3) strongly concave (see Fig. 2).

123. *Accessory mental foramina*: (0) present, in addition to and usually posterior to the large principal foramen; (1) absent (see Fig. 2).

125. *Posterior border of mandible*: (0) descends ventrally or posteroventrally from condyle without marked interruption or abrupt change of direction; (1) bears a steplike process (processus angularis superior) below condyle; (2) has no distinct processus angularis superior but does have broadly convex outline beginning well below condyle (see Fig. 2).

126. *Anterior border of coronoid process*: (0) approximately vertical; (1) extends slightly anterior to base of process; (2) extends very far anterior to base (see Fig. 2).

127. *Mandibular dental capsule*: (0) completely enclosed by bone of mandible; (1) exposed posteroventrally; (2) absent.

128. *Horizontal ramus of mandible*: (0) slender (minimum dorsoventral height < 0.25 × length of mandible); (1) broad dorsoventrally (height 0.25 × length of mandible) (see Fig. 2).

129. *Ventral border of horizontal ramus of mandible*: (0) tangent to angle; (1) not tangent to angle (see Fig. 2).

136. *First upper incisor*: (0) with enamel on all sides, forming complete enamel crown; (1) enamel mainly on lateral side.

137. *First upper incisor*: (0) enamel crown distinct from root; (1) enamel extends entire length of tusk.

138. *First upper incisor*: (0) not strongly curved; (1) strongly curved in parasagittal plane. (Polarity uncertain.)

139. *First upper incisor*: (0) present; (1) vestigial or absent (see Fig. 1).

140. *Depth of I^1 alveolus*: (0) much less than half the length of the premaxillary symphysis; (1) about half the length of the symphysis; (2) much greater than half the length of the symphysis (see Fig. 1).

141. *Cross section of I^1 crown*: (0) suboval or subelliptical; (1) lens-shaped, with sharp anterior and posterior edges; (2) lozenge-shaped (Domning 1978: fig. 3B; 1989a: fig. 4A); (3) broad and extremely flattened mediolaterally (Domning 1990: fig. 4). (Unordered character.)

142. *First upper incisor*: (0) with enamel on all sides, forming complete enamel crown; (1) with enamel mainly on medial side.

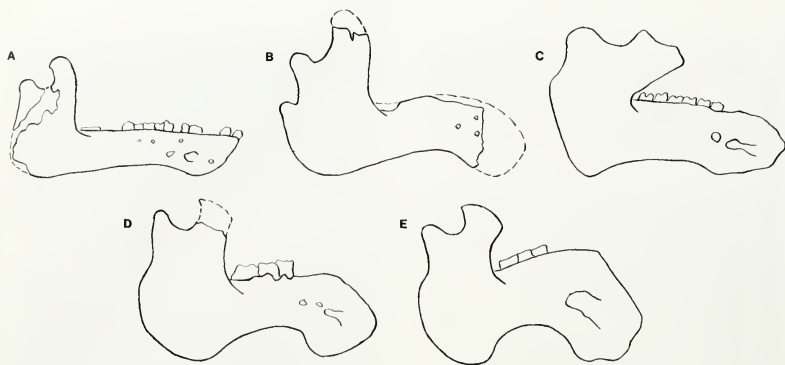143. *Second and third upper incisors, first through third lower*

Figure 2. Right mandibles of sirenians in lateral view, illustrating six of the characters used in this analysis. Not drawn to same scale. See text for explanations of characters and states. A. *Prorastomus sirenoides*: 122(0), 123(0), 125(0), 126(0), 128(0), 129(0). B. *Protherium veronense*: 122(2), 123(0), 125(1), 126(0), 128(0), 129(0). C, *Trichechus senegalensis*: 122(2), 123(0), 125(2), 126(2), 128(0), 129(1). D, *Halitherium schinzii*: 122(1), 123(0), 125(2), 126(1), 128(0), 129(1). E, *Metaxytherium floridanum*: 122(3), 123(1), 125(2), 126(1), 128(1), 129(1).

incisors: (0) present, at least in part; (1) all absent.

144. *Canines*: (0) double-rooted; (1) single-rooted; (2) absent.

146. *Fifth permanent premolars*: (0) present; (1) absent; i.e., no replacement occurs at P^5 and P_5 loci.

150. *Supernumerary molars*: (0) absent and replenished indefinitely by horizontal replacement (Domning 1982).

151. *Functional cheek teeth*: (0) present in adult; (1) present in juvenile only; (2) absent (Domning 1978; Domning and Deméré 1984).

155. *Postcanine dental formula*: (0) P1–4, M1–3; (1) P1–5, M1–3, or secondarily reduced from this condition by loss of anterior premolars. [It is still unresolved whether the five premolars of early sirenians are a synapomorphy of the order, as assumed here, or a retention of a primitive placental trait. However, 1 still lean toward the latter opinion, as expressed in Domning et al. (1982, 1986). In any case the decision would not affect the analysis within the Sirenia since five premolars are clearly primitive for the order. See Thewissen and Domning (1992) for further discussion.]

156. *Cheek-tooth enamel*: (0) smooth; (1) wrinkled.

157. *Permanent premolars*: (0) some double- or triple-rooted; (1) all single-rooted; (2) all absent.

158. *Molars*: (0) unreduced; (1) conspicuously reduced in size relative to skull and mandible, without loss of total occlusal area [as a result of increased number of molars (Domning 1982); however, character state 150(1) also occurs in the absence of this one).

RESULTS OF CLADISTIC ANALYSIS

The analysis of the 36 sirenian taxa using the 62 unweighted characters above and the mh*;bb*; routine (which constructs trees with branch-swapping and retains all trees for each initial one found) in Hennig86 produced 60 maximally parsimonious trees, all of them 152 steps long with a consistency index of 0.55 and a retention index of 0.83. A Nelson consensus tree of these 60 revealed that the variation among them was due entirely to different

combinations of variants in the topology of some Eocene dugongids (node 6 in Fig. 3) and in that of the rytiodontine–dugongine clade (nodes 20–23). The remainder of the tree was stable.

Use of Hennig86's successive-weighting option reduced the number of trees from 60 to 6 and eliminated most of the variation in the rytiodontine–dugongine clade, leaving this part of the consensus tree much better resolved (Fig. 3) and increasing the consistency and retention indices to 0.76 and 0.91, respectively, with a tree length of 162. However, as discussed below, the resolution of the rytiodontine–dugongine clade in Fig. 3 may well be incorrect. Character fits and weights for this consensus tree are given in Table 2.

Because missing data have been shown to cause problems in cladistic analysis (Platnick et al. 1991; Huelsenbeck 1991), I reran the analysis omitting the nine taxa lacking data for 20 or more characters (*Eosiren abeli*, *E. stromeri*, *Ribodon limbatus*, *Potamosiren magdalenensis*, *Anomotherium langewieschei*, *Halitherium christolii*, *Rytiodus capgrandi*, *Corystosiren varguezi*, *Xenosiren yucateca*). The mh*;bb*; routine produced two trees 140 steps long with a consistency index of 0.58 and a retention index of 0.83. Successive weighting reduced these two to a single tree that departed from the topology shown in Fig. 3 in only one respect: *Halitherium schinzii* was shifted downward two nodes, becoming the sister group of the other taxa included within node 8 of Fig. 3 (namely, of the Trichechidae, Dugonginae, *Caribosiren*, *Metaxytherium*, and Hydrodamalinae). In all other respects the tree remained stable.

The character transformations at the nodes of the tree in Fig. 3 (or at terminal taxa within these nodes) are listed below. Also listed are characters (e.g., postcranial characters) not used in the analysis but supporting various parts of this tree. The letters r and c after character-state changes denote reversals and convergences, respectively; the numbers after the letter c indicate the other nodes at which the convergence occurred (or, in the case of convergences in terminal taxa, the nodes under which the convergence is discussed

TABLE 1. Matrix of character-state data for sirenian taxa and outgroups analyzed.

Taxon	Maximum sample size[a]
Moeritherium	2
Palaeoparadoxia	4
Prorastomus sirenoides	–
Protosiren fraasi	6
Eotheroides aegyptiacum	4
Eosiren abeli	–
Protosiren veronense	3
Eosiren libyca	11
Eosiren stromeri	1
Protosiren intermedium	1
Trichechus m. manatus	27
Trichechus m. latirostris	51
Trichechus senegalensis	30
Trichechus inunguis	45
Ribodon limbatus	2
Potamosiren magdalenensis	1
Anomotherium	–
langewieschei	1
Miosiren kocki	1
Halitherium schinzii	22
Halitherium christolii	2
Rytiodus capgrandi	–
Corystosiren varguezi	4
Xenosiren yucateca	1
Dioplotherium allisoni	2
Dioplotherium manigaulti	5
Dugong dugon	65
Crenatosiren olseni	3
Carbosiren tumeri	1
Metaxytherium krahuletzi	4
Metaxytherium medium	2
Metaxytherium calvertense	3
Metaxytherium floridanum	52
Metaxytherium serresii	7
Metaxytherium subapenninum	3
Dusisiren jordani	8
Dusisiren dewana	1
Hydrodamalis cuestae	5
Hydrodamalis gigas	22

[a] Maximum number of specimens of the taxon for which any character was scored.

[b] A dash (–) signifies that the taxon is not applicable to the taxon (Hemig86 treats ? and – alike). Significant polymorphisms are noted and discussed under Results.
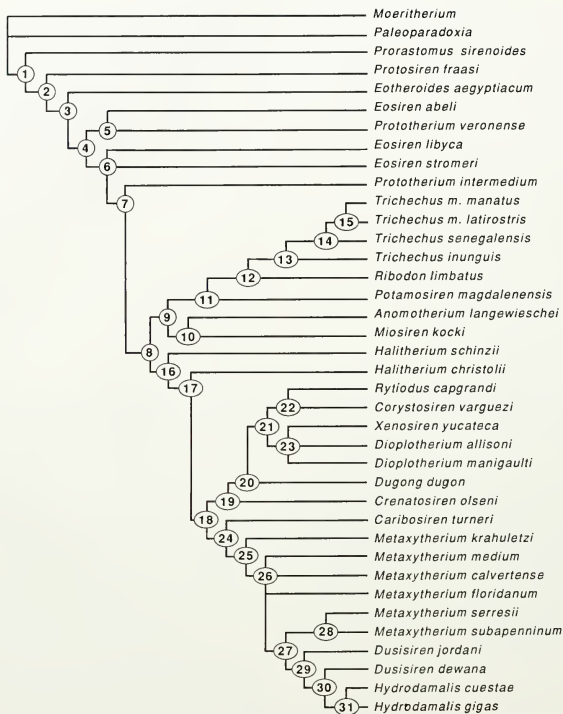
Figure 3. Nelson consensus tree of sirenian taxa and outgroups, generated by Hennig86 using 62 characters and the successive weighting option. Tree length, 162 steps; consistency index, 0.76; retention index, 0.91. Character fits and weights are given in Table 2. Note that node 27 is probably spurious (see text).

below). Autapomorphies of terminal taxa are listed if any are known. When the node at which a transformation occurred is uncertain because of missing data, the transformation is listed under the first node or terminal taxon by which it had certainly occurred, with an indication of the earlier node at which it may questionably have first occurred. Significant polymorphisms are also noted where they occur.

Places where the nodes of the tree correspond to traditionally recognized taxa are indicated. Only one new name is introduced here: inclusion of the Miosireninae within the Trichechidae necessitates the recognition of the new nominotypical subfamily Trichechinae. This and other suggested modifications to the present classification of the taxa here considered are shown in the Appendix.

Basal Radiation of the Sirenia; Prorastomidae

Node 1 (order Sirenia; one branch forms the possibly paraphyletic family Prorastomidae): 8(1), 9(1), 51(1), 155(1). Also, mastoid inflated and exposed through occipital fenestra (Novacek and Wyss 1987); ectotympanic inflated and droplike (Tassy and Shoshani 1988); pachyostosis and osteosclerosis present in skeleton (Domning and de Buffrénil 1991). The possession of five premolars, 155(1), is here provisionally treated as a synapomorphy of the Sirenia rather than a primitive retention, in view of the strong evidence placing the Sirenia well within the Ungulata, which are characterized by only four (Thewissen and Domning 1992). Although possession of double-rooted canines, 144(0), is here treated

TABLE 2. Character fits and weights for the tree in Figure 3.

Character	Steps[a]	Consistency index	Retention index	Weight[b]
3	3	33	77	2
6	1	100	100	10
7	1	100	100	10
8	1	100	100	10
9	1	100	100	10
11	5	20	75	1
13	1	100	100	10
14	5	40	25	1
16	4	25	62	1
31	2	50	91	4
32	4	25	40	1
36	3	66	91	6
37[c]	3	66	80	5
38	1	100	100	10
42	1	100	100	10
43	2	50	75	3
51	1	100	100	10
66	2	50	88	4
67	7	42	82	3
70	3	66	75	5
73	2	100	100	10
74	1	100	100	10
75	1	100	100	10
76	3	33	60	2
77[c]	4	50	83	4
82	2	100	100	10
84	1	100	100	10
85	6	33	84	2
87	2	50	75	3
88	1	100	100	10
89	1	100	100	10
91	5	40	70	2
97	3	66	83	5
99	4	25	72	1
101	1	100	100	10
102	2	50	66	3
103	2	50	75	3
115	1	100	100	10
121	2	50	66	3
122	6	50	85	4
123	4	25	78	2
125	2	100	100	10
126	5	40	62	2
127	2	100	100	10
128	2	50	88	4
129	2	50	90	4
136	1	100	100	10
137	3	33	71	2
138	1	100	100	10
139	2	50	85	4
140	8	25	68	1
141[c]	3	100	100	10
142	2	50	75	3
143	1	100	100	10
144	3	66	90	5
146	1	100	100	10
150	1	100	100	10
151	2	100	100	10
155	1	100	100	10
156	1	100	100	10
157	3	66	93	6
158	1	100	100	10

[a] Number of transformations undergone by the character on this tree.
[b] Calculated by the successive weighting option of Hennig86.
[c] Unordered character.

as a primitive retention in *Prorastomus*, it may be that the same reasoning should apply to this character. Autapomorphies of *P. sirenoides*: 11(1)c5,11,25, 136(1), 137(1)c10,20, 138(1), 140(1)c7,28; also, extension of premaxilla–maxilla suture forward of rear end of premaxillary symphysis; enlargement of P$_1$. Scoring of this species was based on a redescription of the holotype and examination of fragmentary new material (including a tusk) from Jamaica by Savage et al. (in press).

Protosirenidae and Early Dugongidae

Node 2 (one branch forms the possibly paraphyletic family Protosirenidae): 32(1), 67(1), 103(1), 115(1), 122(1), 144(1), 157(1). Also, increase in rostral deflection; reduction of wing of atlas; loss of costal groove on ribs. Autapomorphies of *Protosiren fraasi*: 3(1)c6?, 102(0)r; however, 3(1) here may be spurious, due to distortion (Andrews 1906: 204).

Node 3 (paraphyletic family Dugongidae; paraphyletic subfamily Halitheriinae): 73(1), 75(1), 76(1), 77(1), 101(1), 102(1) (node 1?), 121(1), 125(1) (node 2?), 127(1) (node 2?). Autapomorphy of *Eotheroides aegyptiacum*: 123(1)c10,17. Characters 13 and 82 are derived in exactly half the sample of *E. aegyptiacum* (actual frequencies 1/2 and 2/4, respectively); they were arbitrarily scored here as primitive for this species, which appears to be genuinely transitional in regard to these two characters. Other polymorphisms and frequencies observed in this species: 32(0), 1/3; 67(2), 1/3; and possibly 103(0), 1/3. A fourth specimen, definitely displaying 103(0) according to Abel (1913), was made the type of *Eosiren abeli* by Sickenberg (1934).

Node 4: 13(1), 82(1), 97(1), 146(1) (node 3?). Also, reduction of pubis and probable loss of terrestrial locomotor ability (node 3?).

Node 5: 141(1). Autapomorphies of *Prototherium veronese*: 11(1)c1,11,25, 32(0)rc10, 67(0)rc14, 121(0)r, 122(2)c11,29; also, pronounced narrowing of skull roof. Polymorphism and frequency observed: 76(0), 1/2. I scored the processus retroversus as present, 77(1), in *P. veronese*, contrary to Sickenberg (1934). The holotype of *Eosiren abeli* was destroyed in World War II; scoring of this species is based on the description by Sickenberg (1934) and on unpublished new material provisionally referred to this species.

Node 6: 3(1)c2?, 67(2), 91(1) (node 4?), 126(1) (node 2?). Also, broadening of supraspinous fossa of scapula; loss of symphyseal contact between pubic bones. Polymorphisms and frequencies observed in *Eosiren libyca*: 32(0), 1/11; 43(1), 1/8; 122(2), 1/4. Autapomorphies of *E. stromeri*: frontals much longer than parietals in midline; M^3 smaller than M^2.

Node 7: 125(2), 140(1)c1,28.

Node 8: 143(1), 144(2).

Trichechidae

Node 9 (family Trichechidae): 3(0)r, 77(0)rc31, 82(2); also, reduction of neural spines; possible tendency to enlargement and (at least in *Trichechus*) anteroposterior elongation of thoracic centra.

Node 10 (subfamily Miosireninae): 32(0)rc5, 38(1). Possible autapomorphy of *Anomotherium langewieschei*: 123(1)c3,17 (node 10?). Autapomorphies of *Miosiren kocki*: 16(1)c12,20 (node 10?), 36(1)c18, 73(2), 85(2)c20,26 (node 10?), 97(0)r (node 10?), 137(1)c1,20 (node 9?), 140(2)c20,28 (node 10?); also, reduction and simplification of M^3.

Node 11 (subfamily Trichechinae): 11(1)c1,5,25, 99(1)c27, 122(2)c5,29, 157(2)c18; also, thickening of molar enamel (node 9?) (Domning, in press). *Potamosiren magdalenensis* is here taken to include *Metaxytherium ortegense* (Domning, in press).

Node 12: 16(1)c10,20, 150(1); also, thinning of molar enamel (reversal; Domning, in press). *Ribodon limbatus* is here taken to include the maxilla (U.S. National Museum 167655) referred to *Ribodon* sp. by Domning (1982).

Node 13 (genus *Trichechus*): 31(1)c18 (node 11?), 67(1)rc22 (node 11?), 91(2)c29 (node 11?), 126(2) (node 9?), 139(1)c29 (node 11?), 140(0)rc24 (node 11?), 158(1). Also, reduction of cervical vertebrae to six (node 11?); elongation of acromion process of scapula (node 9?); reduction of bicipital groove of humerus (node 11?); reduction of ilium (node 11?). Polymorphisms include 11(0) in all species, 67(0), 84(1), 99(0), 129(1), and 156(1) in *T. inunguis*, 156(0) in *T. manatus*, 156(1) in *T. senegalensis*, and 67(1), 84(0), 122(1), and 129(0) in both *T. manatus* and *T. senegalensis*; the frequencies of these states have not been determined in all cases. Autapomorphies of *T. inunguis*: 70(1)c29; also, division of foramen incisivum; lateral projection of temporal crests with postorbital apophyses on frontal frequent; inflation of supraoccipital; elongation of mandibular symphysis; increase in number of accessory mental foramina; reduction of DP[3] and DP[4]; increase in complexity and further decrease in size of molars; reduction of thoracic vertebrae to 14–16; elongation of forelimb; loss of nails. See Domning and Hayek (1986) for details regarding *Trichechus*.

Node 14: 67(0)rc5, 84(1), 129(1)c16. Also, loss of bicipital groove of humerus. Autapomorphies of *Trichechus senegalensis*: shortening of rostrum; decrease in rostral deflection; more transverse orientation of posterolateral sides and constriction of bases of supraorbital processes; presence of longitudinal crests on floor of mesorostral fossa; broadening of zygomatic arch and coronoid process.

Node 15 (*Trichechus manatus*): 156(1). Also, elongation of vomer; more transverse orientation of median portion of frontoparietal suture; broadening of ribs. Autapomorphies of *T. m. latirostris*: widening of foramen magnum and straightening of its dorsal border; increase in rostral deflection; increase in height of mandibular symphysis.

Later Dugongidae

Node 16 (paraphyletic genus *Halitherium*): 85(1) (node 8?), 129(1)c14. Also, development of cetaceanlike triangular flukes in place of a rounded caudal fin. Polymorphism and frequency observed in *H. schinzii*: 13(0), 4/6; though in the majority, this state has an LCL₉₅ of only 0.223, and is also incongruent.

Node 17: 122(3), 123(1)c3,10, 128(1).

Node 18: 31(1)c13 (node 17?), 36(1)c10, 157(2)c11 (node 17?).

Dugonginae, Including Rytiodontinae

Node 19 (subfamily Dugonginae, formerly Rytiodontinae): 37(1), 43(1), 88(1). Autapomorphies of *Crenatosiren olseni*: fusion of nasals with frontals; elongation of bases of supraorbital processes; deepening of nasal incisure.

Node 20: 16(1)c10,12, 42(1), 85(2)c10,26, 137(1)c1,10, 140(2)c10,28, 142(1). Autapomorphies of *Dugong dugon*: 14(1)c26,31, 37(2)c22, 43(0)r, 66(1)c26; also, strong inflection of processus retroversus of squamosal; constant presence in juveniles of deciduous I[1], and frequent presence in adults of vestigial lower incisors (these are atavisms, seemingly due to neoteny); sexual dimorphism in size and eruption of permanent I[1] tusks; functional loss of enamel crowns of cheek teeth; persistently open roots of M[2–3] and M₂,₃. Although the zygomatic process of the jugal of the adult *Dugong* is long, 89(0), the process is much shorter in fetuses and neonates, suggesting that the ancestors of *Dugong* may have had the derived state 89(1), like *Dioplotherium* and *Xenosiren* (below). *Trichechus*, in contrast, has a long process in both fetuses and adults, so a short process is not simply a condition of early ontogeny.

Node 21: 6(1), 141(2).

Node 22: 7(1), 141(3). Autapomorphies of *Corystosiren varguezi*: 37(2)c20, 67(1)rc13 (node 22?), 76(0)rc23. Separation of

the squamosal from the temporal crest, 76(0), may reflect the great and uniquely derived thickening of the parietals characteristic of *Corystosiren*.

Node 23: 89(1). Also, incipient blockage of infraorbital canal by a transverse wall; apparent fusion of nasals with frontals. Autapomorphies of *Dioplotherium manigaulti*: 16(1)r?, 97(2), 142(0)r?; these "reversals" more likely indicate that this entire clade should be rooted farther down in the tree. Possible autapomorphies of *D. allisoni*: 76(0)rc22 (condition unknown in its possible descendant *Xenosiren*); 123(0)r (node 21?). *D. allisoni* here includes referred specimens from Brazil (Toledo and Domning 1991). Autapomorphies of *X. yucateca*: 14(2), 85(1)r; also, accentuation of concavity of frontal roof; thinning and medial concavity of preorbital process of jugal.

Caribosiren and *Metaxytherium*

Node 24: 140(0)rc13. It is uncertain whether the tusks of *Caribosiren* were really absent (an autapomorphy) or merely small.

Node 25 (paraphyletic genus *Metaxytherium*): 11(1)c1,5,11. See Domning and Thomas (1987) and Domning (1988) for details. Polymorphism and frequency observed in *M. krahuletzi*: 66(1), 1/2; evidently a genuinely transitional condition, scored arbitrarily as primitive.

Node 26: 66(1)c20, 85(2)c10,20. Autapomorphy of *Metaxytherium floridanum*: 14(1)c20,31. Polymorphisms and frequencies observed in *M. floridanum*: 11(0), 8/26, 14(0), 1/3; 67(1), 15/26; 85(1), 12/20. The latter two majority states have LCL₉₅s of only 0.369 and 0.361, respectively, and are both incongruent.

Node 27: 67(3), 99(1)c11. I believe that this node is spurious and that these changes were actually evolved in parallel by European Pliocene *Metaxytherium* and North Pacific hydrodamalines (i.e., at nodes 28 and 29 of this tree, respectively).

Node 28: 140(1)rc1,7; this increase in tusk length was interpreted by the program as a re-reversal of the reduction at node 24. The body of *M. serresii* is smaller than that of the European Miocene *Metaxytherium*; I interpret this as ecophenotypic dwarfism that was reversed in *M. subapenninum* (Domning and Thomas 1987). Polymorphisms and frequencies observed: in *M. serresii*, 31(0), 2/3; in *M. subapenninum*, 66(0), 2/3. In each case, the majority state has an LCL₉₅ of only 0.094 and is incongruent. Autapomorphy of *M. subapenninum*: 140(2)c10,20. This name is accepted by Pilleri (1988) as a valid senior synonym of *M. forestii*.

Hydrodamalinae

Node 29 (subfamily Hydrodamalinae; paraphyletic genus *Dusisiren*): 70(1)c13, 77(2), 87(1), 91(2)c13, 122(2)rc5,11, 128(0)r, 139(1)c13. Also, decreased rostral deflection; increased body size (to about 4.5 m in *D. jordani*). See Domning (1978) for details. Polymorphisms and frequencies observed in *D. jordani*: 66(0), 2/6; 67(1), 1/5. A peculiarity of the available specimens of *D. jordani* is separation of the palatines in the midline, a condition seen in no other sirenian. Although the palatal incisure is consequently very deep, because of the different anatomical basis of this condition (compared to *Dioplotherium manigaulti*, where the incisure is deep despite the median juncture of the palatines), character 97 here was scored 1 rather than 2. Whether this separation of the palatines is a true autapomorphy that rules *D. jordani* out of the ancestry of later species, or whether this condition was later reversed or occurred here only as an individual variation, needs to be addressed by future work.

Node 30: 74(1). Also, reduction in complexity of molars; broadening of manubrium; development of keel on xiphisternum; narrowing of supraspinous fossa of scapula; increased circularity of humeral head; reduction of deltoid crest; medial bowing of radius–

ulna; extensive modifications of carpals; reduction of metacarpals and phalanges. See Takahashi et al. (1986) for details.

Node 31 (genus *Hydrodamalis*): 14(1)c20,26, 151(1). Also, presence of dentiform process on premaxilla; more nearly rectangular shape of rostral masticating surface; broadening of lateral side of pterygoid process; concealment of infraorbital foramen in ventral view; reduced indentation of squamosal at mastoid foramen; inflation of pars temporalis of periotic; reduced curvature of coronoid process of mandible; upward extension of a vertical anteromedial ridge almost or quite into coronoid process; extension of ligamentary notch to center of humeral trochlea (node 30?); increased proximal curvature of anterior ribs; increased body size (to 7–10 m). Polymorphism and frequency observed in *H. cuestae*: 77(0), 2/5; this is a genuinely transitional condition. Autapomorphies of *H. gigas*: 36(2), 70(2), 77(0)rc9, 126(0)r, 127(2), 151(2); also, subrectangular shape of rostral masticating surface; sharp anterior demarcation of foramen incisivum; loss of tentorium ossium and bony falx cerebri; presence of deep pits in anterodorsal roof of braincase; shorter and higher shape of cranial cavity, and elevation of roof well above crista galli; rounding of cranial vault (reduction of temporal crests); more ventral placement of optic foramina relative to sphenorbital fissures; broadening of posterior end of squamosal zygomatic process and rounding of its outline; rugosity of surface of periotic; reduction or loss of coronoid canal of mandible; more posterior placement of mental foramen; square rather than rhomboid sagittal sections of thoracic vertebrae 1 and 2; straight or irregularly concave anterior border of scapula; reduction of acromion and its elevation well above glenoid fossa of scapula; restriction of ligamentary attachment to center of humeral trochlea; opening of notch for this ligament on radius–ulna toward medial rather than lateral side. Polymorphisms and frequencies observed in *H. gigas*: 14(0), 1/18; 66(0), 1/17. See Domning (1978) and Domning and Deméré (1984) for details.

DISCUSSION

Age and Clade Ranks.—A gratifying aspect of this analysis is the close correspondence between the geological ages of the taxa and their positions on the tree. The earliest known sirenian, *Prorastomus* (early and middle Eocene; Donovan et al. 1990), also stands at the base morphologically, and is followed by the other middle Eocene forms (*Protosiren, Eotheroides, Eosiren abeli*). *Prototherium* and the other *Eosiren* species are late Eocene. Node 8 comprises exclusively post-Eocene taxa; the clean Eocene–Oligocene separation on the tree is probably due in part to the lack of any named early Oligocene sirenians in the fossil record. Node 9 defines a clade including one late Oligocene form (*Anomotherium*) and seven Neogene ones; *Potamosiren, Ribodon,* and *Trichechus* are arrayed in known stratigraphic order. *Halitherium schinzii* and *Caribosiren* are middle Oligocene; *H. christolii, Crenatosiren,* and *Dioplotherium manigaulti* are late Oligocene. *D. allisoni* and *Rytiodus* appeared in the early Miocene, *Corystosiren varguezi* and *Xenosiren yucateca* in the late Miocene or Pliocene, while the Recent *Dugong* doubtless had a long but still unknown fossil record. The species of *Metaxytherium* are in known stratigraphic order from the early Miocene *M. krahuletzi* through the three middle Miocene species to the Pliocene *M. serresii* and *M. subapenninum*. Finally, *Dusisiren* diverged from *Metaxytherium* before the late Miocene and gave rise to *Hydrodamalis* by the end of the Miocene. Hence this tree could be converted into a plausible phylogram with only minor adjustments.

Norell and Novacek (1992) presented an improved method for quantifying the fit between age and clade rank, and Fig. 4 displays the data above graphically for comparison with the taxa Norell and Novacek used as examples. The correlations are highly significant for the Sirenia shorn of the major side branches Trichechidae and Dugonginae, and for the Trichechidae considered separately. Not surprisingly, the correlation for the Dugonginae is nonsignificant, largely because *Dugong dugon*, the second-earliest member of the group in terms of clade rank, is a Recent species with no fossil record. (For the purposes of this analysis, the family Trichechidae includes *Anomotherium* from the miosirenine side branch because it is the earliest taxon assigned to the family but excludes *Miosiren* in order to simplify the topology of the portion of the tree being analyzed. *Anomotherium* was also included in the "Most Sirenia" analysis together with *Crenatosiren; Eosiren abeli* and *Metaxytherium subapenninum* were omitted to simplify the topology.)
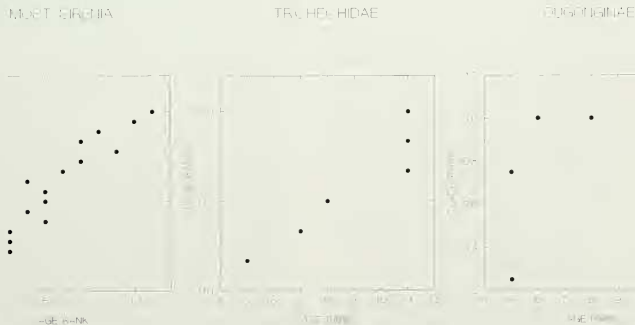

Figure 4. Plots of age ranks as a function of clade ranks for subsets of the Sirenia (see text for taxa included). Clade ranks are rescaled from 0 to 1. Correlations are statistically significant (S, Spearman rank correlation coefficient) for "Most Sirenia" exclusive of most Trichechidae and Dugonginae ($S = 0.974$, $P < 0.0001$) and for the Trichechidae ($S = 0.915$, $P < 0.002$), but not significant for the Dugonginae ($S = 0.263$).

The "Dugonginae" analysis included *Crenatosiren*, *Dugong*, *Dioplotherium manigaulti*, *Rytiodus*, and *Corystosiren*. Some data points on the scatter diagrams coincide.)

The highly significant correlations obtained in the two most inclusive of these analyses confirm the generally impressive effectiveness and reliability of the sirenian fossil record in recovering the sequence of phylogenetic divergences. These results are comparable to those presented by Norell and Novacek (1992) for most subdivisions of the Perissodactyla, a group thought to have a relatively complete and well-understood fossil record. With the obvious and important exception of the Dugonginae, then, it appears that the sirenian fossil record is not grossly deficient in the picture it provides of this group's history.

Comments on individual nodes.—The characters uniting all sirenians at node 1 have been discussed above. *Prorastomus* is traditionally, and justifiably, regarded as close to the ancestry of all other sirenians and placed in its own monotypic and probably paraphyletic family. It appears to possess several derived features that exclude it from the direct ancestry of other taxa. However, these characters are not well understood and some of them are based on a referred tusk (Savage et al., in press) whose identification might be questioned, so it remains to be seen just how close *Prorastomus* actually is to the base of the sirenian radiation. Meanwhile, it is by far the closest thing we have to a structural ancestor for other sirenians, and it should be used wherever possible to represent the Sirenia in interordinal comparisons.

Protosiren, at node 2, has likewise been accorded its own, probably paraphyletic family, and with at least two undescribed genera it seems to represent a grade of evolution intermediate between *Prorastomus* and other sirenians. Its possession of at least one character state seemingly more primitive than seen in *Prorastomus* [absence of a pterygoid fossa, 102(0)] is puzzling, and there may be some problem in definition or interpretation of this character.

The position of *Eotheroides* (node 3) was very stable throughout the analysis; it has generally been considered the most primitive dugongid. In the past the name *Eotheroides* has sometimes been applied instead (by myself as well as others) to all the species here placed in *Eosiren*; here *E. aegyptiacum* is provisionally maintained in its own genus, pending better knowledge of this and related forms and a thorough revision of Eocene taxa.

Nodes 4–7 are rather unstable, and this part of the tree should be considered provisional; the Eocene dugongids are badly in need of thorough revision. Node 5 is supported by only one character, which is weakly attested by specimens. The position of *Prototherium veronense* is especially problematical because this species displays several very primitive states, here interpreted as reversals. *Prototherium intermedium* (node 7) was consistently separated from *P. veronense* and should not be considered congeneric with it; the monophyly of *Eosiren* is also open to question. Better knowledge of all Eocene sirenians (of which many poorly known nominal taxa were excluded from this study) will probably change this part of the tree drastically.

Node 8, as noted above, includes all the post-Eocene sirenians and seems to mark the point at which the manatees separated from the dugongs. This separation has long been dated to the Eocene, but this analysis implies a later rather than earlier Eocene (and conceivably even an early Oligocene) divergence. The hypothesis (e.g., Domning 1982) of a protosirenid origin for manatees separate from that of the dugongids is decisively refuted by this analysis: the trichechid clade is stably rooted within the Dugongidae as traditionally defined.

On the other hand, my suggestion (in Barnes et al. 1985) that *Anomotherium* and *Miosiren* (node 10) are closer to manatees than to other sirenians is supported by these results (node 9), as is my

previous interpretation of manatee phylogeny (nodes 11–15; Domning 1982; Domning and Hayek 1986). It seems opportune to include the Miosireninae formally within the Trichechidae, necessitating the introduction here of the name Trichechinae for the contents of the Trichechidae as previously understood.

The well-known European mid-Oligocene species *Halitherium schinzii* appears to be the sister group of all later dugongids (node 16). *H. christolii* occupies a similarly significant position one rung higher (node 17), so it is particularly unfortunate that this species from the late Oligocene of Austria is so poorly known. *H. christolii* could be interpreted as a structural ancestor of the rytiodontine–dugongine clade as well as of *Metaxytherium* and the hydrodamalines (node 18), but in fact many of its character states are unknown and judgment on this point should be reserved.

The subfamily Rytiodontinae (node 19), whose validity I questioned as recently as 1985 (Barnes et al. 1985), has since proven to represent a major adaptive radiation beginning in the late Oligocene and apparently centered in the Caribbean and western Atlantic (Domning 1989a,b, 1990, 1991). Perhaps the most significant finding of this study is that *Dugong* is stably located within the rytiodontine clade (node 20). This conclusion needs to be corroborated by more fossils from the Indo-Pacific region where *Dugong* presumably evolved. However, it is the first strong indication of where in sirenian phylogeny the affinities of the modern dugong might lie, and it justifies combining the Rytiodontinae and the previously monotypic Dugonginae into a single subfamily, which must under the principle of priority take the latter name.

Although the consensus tree derived from the Hennig86 successive weighting routine resolved the remainder of the rytiodontine clade (nodes 21–23) in a way generally supportive of my previous conclusions (Domning 1989a,b, 1990), this is the least stable part of the entire tree, and any of the possible most-parsimonious arrangements involve several parallelisms and/or reversals. The reason for this instability lies in the fact that study of this group of sirenians is just beginning; several key specimens and new taxa have yet to be described, and several of the named taxa are scored on the basis of unique, fragmentary, and/or doubtfully referred specimens. As with the Eocene dugongids, greater clarity can be expected to emerge over the next few years.

The position of *Caribosiren* (node 24) was one of the least stable through the preliminary analyses; the genus is represented by only a single well-preserved but incomplete skull for which several characters cannot be scored. Its apparent middle Oligocene age also tends to cast doubt on its present position in the tree. Conversely, its horizon may actually be late Oligocene, which would improve the correlation between its age and clade ranks.

Node 25 defines the well-known and widely distributed genus *Metaxytherium*, and nodes 26 and 28 corroborate my earlier interpretation of *M. krahuletzi–M. medium–M. serresii–M. subapenninum* as an Old World phyletic series (Domning and Thomas 1987). New evidence, however, casts doubt on the origin of the genus from European *Halitherium christolii*, and the New World *Metaxytherium* species themselves are far from satisfactorily understood. Supporting a New World origin for the genus is its nearest sister taxa (*Caribosiren*, *Crenatosiren*) being New World forms, and the next taxon (*H. christolii*) may also be represented in North America. Furthermore, the oldest specimens of *Metaxytherium* itself now appear to be ones from the late Oligocene of the southeastern U.S. However, their small size is incongruent with the larger size of most of their likely ancestors and descendants. There are also problems of species definition as well as synonymy involving the middle Miocene *M. calvertense*, and this species and the somewhat later *M. floridanum* are difficult to separate from near-contemporary European and eastern Pacific forms (cf. Domning 1988; Aranda-Manteca, Domning, and Barnes 1994, this

volume). This is another part of the tree urgently needing attention. *M. calvertense* has been proposed as the sister group and ancestor of *Dusisiren* (Muizon and Domning 1985; Aranda-Manteca, Domning, and Barnes 1994, this volume).

Node 27, which unites the Pliocene *Metaxytherium* of Europe with the late Miocene and later hydrodamalines of the North Pacific, I consider spurious on zoogeographic grounds. I believe that if node 26 were properly resolved, some sort of division between Old and New World species would appear there, and the minor characters [loss of supracondylar fossa, 67(3); shortening of palatines, 99(1)] that support node 27 would be revealed as having evolved in parallel in the Mediterranean and North Pacific. The species of *Metaxytherium* are a particular focus of my continuing research.

Node 29 defines the Hydrodamalinae, whose successive evolutionary stages leading to the recently extinct Steller's sea cow (*Hydrodamalis gigas*) are supported by numerous character transformations (nodes 30–31).

Molecular vs. morphological phylogeny.—Finally, mention should be made of the sole attempt so far at a sirenian phylogeny based on molecular data (Rainey et al. 1984). These authors conducted immunological comparisons using antisera to bone extracts of *Hydrodamalis gigas* and all four living sirenian species, as well as antisera to serum albumins of the dugong, the Florida manatee, and the Indian and African elephants.

Although their phylogeny of the Recent species agrees topologically with the paleontological consensus, their inferred ages for the most important branch points are inconsistent with the fossil data. They dated the dugongid–trichechid divergence to 17–20 Ma (early Miocene), as opposed to the 30–40 Ma (late Eocene or early Oligocene) date inferred here. They also dated the *Dugong–Hydrodamalis* divergence to 4–8 Ma (late Miocene or early Pliocene), whereas the present (and previous) results suggest a divergence not later than late Oligocene (> 25 Ma).

Rainey et al. (1984) downplayed the seriousness of these contradictions, stating that "none of this is in conflict with the actual fossil record." In reality, they misconstrued several details of the fossil record, most notably in stating that "the first good hydrodamaline (*Hydrodamalis cuestae*) occurs in the 4–8 Ma range." Apart from ignoring *Dusisiren* spp. being cladistically "good" (and much older) hydrodamalines, their reasoning implies that *Dugong* could have been derived from a hydrodamaline only 4–8 Ma old (i.e., from *H. cuestae*). As is clear from the data presented here, this is unparsimonious to an absurd degree. Rainey et al. concluded that their data "should provide a useful framework for further interpretation of the sirenian fossil record." This bold prediction has not come true.

COMMENTS ON METHODS

A peculiar, and surprisingly primitive, feature of contemporary phylogenetic systematics is its extreme typology. Most published cladistic analysts do not state how many specimens of each taxon were examined; in very many cases (especially in studies of fossil vertebrates) the sample size is probably one. Neither do most authors take any particular notice of individual variation, if indeed they have observed it in their samples. [The study by Hulbert and MacFadden (1991) was exceptional in that these authors at least acknowledged variation and stated how they dealt with it, by reporting the state observed in the majority of a sample.] The problem of polymorphisms in supraspecific terminal taxa has been addressed theoretically by Nixon and Davis (1991) and a few other recent authors whom they cited, but they specifically excluded from consideration the more fundamental problem of within-population polymorphisms. Smouse et al. (1991) have shown that intraspecific

variation in DNA can have significant effects on phylogenetic analyses, but there has as yet been no attempt to relate the scoring of characters to any statistical measures of intrapopulational variability, or to attach confidence limits, based on sample size, to the scorings used in an analysis, let alone to the results of the analysis as a whole. In any other branch of modern biology or systematics, particularly evolutionary systematics, this habitual disregard of quantitative methods and lack of population-based thinking would be unacceptable.

For some years I have tried to improve on this approach, at a minimum by reporting sample sizes and patterns of intrapopulational variation in the taxa being analyzed (Domning and Hayek 1986; Domning and Thomas 1987). Here I have proposed an objective method for using such data to make scoring decisions in ambiguous cases. I do not expect that this particular method will prove to be more than a first approximation to what is needed; however, I do hope that its proposal will at least call attention to the need and prompt some discussion of the problems.

The first and most fundamental problem requiring discussion is the frequency that a derived character state should attain in a population before the population as a whole is deemed to be derived: 1%? 51%? 99%? 100%? There is no consensus at present on what choice would be most biologically meaningful, let alone practical. I have arbitrarily chosen "more than 50%."

A second and distinct problem: how confident do we need to be (on the basis of *available sample* size) that the frequency in the *original population* was in fact more than 50% (or whatever frequency we prefer)? I have chosen a 95% confidence level because this is customary in much scientific work and because a higher standard is more difficult to attain; e.g., a 99% confidence level requires a minimum sample size of eight (a 95% confidence level six), even for a completely monomorphic sample. That is, 6/6 is the smallest value of X/n whose LCL_{95} is greater than 0.50 (specifically, about 0.54); a sample of only five, with *no* variation ($X/n = 5/5$), has an LCL_{95} of only about 0.48. This means that for any sample smaller than six, we cannot be 95% certain that any particular state, even one that is constant in the sample, was found in a majority of the original population. (For sample sizes up to 20, the minimum frequencies having an LCL_{95} ≥ 0.50 are as follows: 6/6, 7/7, 8/8, 8/9, 9/10, 10/11, 10/12, 11/13, 12/14, 12/15, 13/16, 13/17, 14/18, 15/19, 15/20.)

It should be emphasized that since the justification for this procedure derives from the phenomenon of intrapopulational variation, the procedure is not applicable to terminal taxa that are supraspecific. However, when the terminal taxa in an analysis are supraspecific ones, it is obviously all the more imperative that their diversity be sampled by the examination of more than one specimen each. Future work will have to determine whether statistics of this sort are of real value in deciding character scorings in borderline cases and whether they can eventually provide a means of placing numerical confidence limits on entire cladograms. The latter task, at least, I leave to others more mathematically skilled than myself. However, I cannot believe that quantitative measures of sample size and of variation—the raw material of evolution—have no relevance to phylogenetic analysis.

CLASSIFICATION

The revised classification of sirenians (see Appendix) should be regarded as merely provisional. In the interest of taxonomic conservatism, it incorporates as few as possible of the changes that could be inferred from this preliminary cladistic analysis, namely, the formal assignment of the Miosireninae to the Trichechidae and the union of the Rytiodontinae with the Dugonginae. In other respects the suprageneric classification of Simpson (1945) is unchanged. As

a result, the Dugongidae and Halitheriinae are conspicuously paraphyletic, and I regard the Prorastomidae and Protosirenidae as probably paraphyletic also, not to mention several of the genera.

While I have no philosophical objection to paraphyletic taxa, I would agree that this classification is unsatisfactory. Any further rearrangements or redefinitions of suprageneric taxa, however, should await further advances in our knowledge, specifically in two of the problematic areas pointed out above: the Eocene dugongids (and Eocene sirenians in general), and the species and relationships of *Metaxytherium*. These, as well as the still incompletely resolved dugongine clade, are topics on which I am actively working, and I fully expect that these parts of the present tree will change in topology in the relatively near future. For this reason I refrain from formalizing the present tree topology in a cladistic classification by use of any of the conventions that have been proposed (sequencing, plesions, etc.), since such a classification would almost inevitably be highly unstable. Users of the present classification who wish to retrieve its cladistic content are referred to Fig. 3.

ACKNOWLEDGMENTS

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APPENDIX: SIRENIAN CLASSIFICATION

The following provisional classification includes the currently correct names for all the genera, species, and subspecies included in this analysis, together with the higher taxa to which they are traditionally or newly assigned. For the original sources of the names of fossil taxa, the reader is referred to the *Bibliography of Fossil Vertebrates*.

ORDER SIRENIA Illiger, 1811
  FAMILY PRORASTOMIDAE Cope, 1889 [paraphyletic?]
    Prorastomus Owen, 1855
      P. sirenoides Owen, 1855
  FAMILY PROTOSIRENIDAE Sickenberg, 1934 [paraphyletic?]
    Protosiren Abel, 1907
      P. fraasi Abel, 1907
  FAMILY TRICHECHIDAE Gill, 1872 (1821)
    Subfamily Miosireninae Abel, 1919
      Anomotherium Siegfried, 1965
        A. langewieschei Siegfried, 1965
      Miosiren Dollo, 1889
        M. kocki Dollo, 1889
    Subfamily Trichechinae Gill, 1872 (1821) [new rank]
      Potamosiren Reinhart, 1951
        P. magdalenensis Reinhart, 1951 [here includes *Metaxytherium ortegense* Kellogg, 1966]
      Ribodon Ameghino, 1883
        R. limbatus Ameghino, 1883

      Trichechus Linnaeus, 1758
        T. inunguis (Natterer in von Pelzeln, 1883)
        T. manatus Linnaeus, 1758
          T. m. manatus Linnaeus, 1758
          T. m. latirostris (Harlan, 1824)
        T. senegalensis Link, 1795
  FAMILY DUGONGIDAE Gray, 1821 [paraphyletic]
    Subfamily Halitheriinae Carus, 1868 [paraphyletic]
      Eotheroides Palmer, 1899
        E. aegyptiacum (Owen, 1875)
      Prototherium de Zigno, 1887
        P. veronense (de Zigno, 1875)
        "*P.*" *intermedium* Bizzotto, 1983 [should probably not be included in this genus]
      Eosiren Andrews, 1902
        E. abeli Sickenberg, 1934
        E. libyca Andrews, 1902
        E. stromeri (Sickenberg, 1934)
      Halitherium Kaup, 1838
        H. schinzii (Kaup, 1838)
        H. christolii Fitzinger, 1842 [here includes *H. abeli* Spillmann, 1959, and *H. pergense* (Toula, 1899)]
      Caribosiren Reinhart, 1959
        C. turneri Reinhart, 1959
      Metaxytherium de Christol, 1840
        M. krahuletzi Depéret, 1895
        M. medium (Desmarest, 1822)
        M. serresii (Gervais, 1847)
        M. subapenninum (Bruno, 1839) [here includes *M. forestii* (Capellini, 1872)]
        M. calvertense Kellogg, 1966
        M. floridanum Hay, 1922
    Subfamily Dugonginae Gray, 1821 [here includes Rytiodontinae Abel, 1914]
      Crenatosiren Domning, 1991
        C. olseni (Reinhart, 1976)
      Dugong Lacépède, 1799
        D. dugon (Müller, 1776)
      Dioplotherium Cope, 1883
        D. manigaulti Cope, 1883
        D. allisoni (Kilmer, 1965)
      Xenosiren Domning, 1989
        X. yucateca Domning, 1989
      Corystosiren Domning, 1990
        C. varguezi Domning, 1990
      Rytiodus Lartet, 1866
        R. capgrandi Lartet, 1866
    Subfamily Hydrodamalinae Palmer, 1895 (1833)
      Dusisiren Domning, 1978
        D. jordani (Kellogg, 1925)
        D. dewana Takahashi, Domning, and Saito, 1986
      Hydrodamalis Retzius, 1794
        H. cuestae Domning, 1978 [here includes *H. spissa* Furusawa, 1988]
        H. gigas (Zimmermann, 1780)